

REPRODUCTION, DISPERSAL AND MIGRATION

1. Ecological and Evolutionary Factors in Sex
2. Migration
3. Larval Dispersal: The Long and the Short Haul
4. Planktonic Larvae: Obstacles to the Final Destination
5. The Macroscale: Major Separations Lead to Biogeographic Structure

Reproduction is the replication of individuals necessary for the population growth, it can be:

- Sexual → occur with the reproduction of sexual gametes
- Asexual → occur without reproduction of sexual gametes

Dispersal is the spread of progeny from one location to another, usually to locations that differ from that of the parent, the dispersion can be caused by:

- One-way process controlled by water currents → in just in one direction, but when the larva became adult it could come back (two-ways process)
- Long distance (it occur also hundreds of Km)
- Passive movement → it depends on the water currents, the large don't use appendices and energy

Migration is a directed movement between specific areas, when the larva is developed an adult

- Allows an expansion of types of habitat use and can increase a species efficiency at exploiting the best resources at optimal feeding and spawning sites, they use energy
- Active movement → reaching different areas, e.g spooning area (where they can reproduce), feeding area (they grow as adult)

All these 3 processes are used to reach 4 important aims:

- Grow and exploit new resource
- increase the size of the population
- Increase the distribution of the species
- Colonize new habitats

1 – ECOLOGICAL AND EVOLUTIONARY FACTORS IN SEX

SEXUAL REPRODUCTION

Benefits of sexual reproduction

Producing new organisms, offsprings which are different to their parents

Why the evolution bring the organisms to use sex to reproduce then the asexual reproduction that doesn't involve energy? (Find a mate, fight with other male, give nutrition to the progeny...) because there is the **generation of GENETIC DIVERSITY.**

- ✓ Sex increases combinations of genes
- ✓ Increase the ability of the offspring to survive and exploit a wide variety of habitats, to have the ability to adapt to the environmental change
- ✓ Increased evolutionary potential when the environment changes (the ability to cope with stressors)
- ✓ Confers resistance to diseases

e.g. Fiddler crab *Uca*, have one large claw used only for sexual displays and combat but not for feeding. Thus, males must compensate for this handicap by feeding longer and faster

Sexual selection process is involved

- ✓ Selection for secondary sex features that increase the mating success
- ✓ Selection for extreme forms that breed more successfully
- ✓ This sexual selection can involve selection for display conspicuous coloration, enhanced combat structures (e.g. Fiddler crab *Uca* : one of the due clone is used to attract female, bigger is the clone, higher is the capacity to attract them and combat with other male) , larger body size

GOOD GENES HYPOTHESIS: *it proposes that females select males that seem to have genetic advantages that increase offspring quality*

- e.g. the major claw of fiddler crabs is employed for display to attract females and for combat with other males
- e.g. bright coloration in male fishes

An experiment to demonstrate that females prefer larger males related to the sexual selection

They create a mirror with 2 side, one side reflects the normal image (body of the crab), the other magnify the semi image (increasing the size of the body of then Crab). They put the male between the 2 side in order to allow the female to see only the relation of the male → female prefers the biggest male, she was always attract by the magnify image of the crab to confirm that the sexual selection is important and many morphological treats of the male can affect the sexual selection.

Types of sexuality

We can divide organisms:

MONOCHORISTIC SPECIES → ASK DURING THE EXAM

- species with have separate sexes (e.g. we are gonochoristic species)
- in animals, this characteristic entails the need for a mechanism of sperm transfer (these species, which do sexual reproduction, *must have a mechanism to transfer the sperm/the gametes between the two sexes*). *Since we are in the marine environment, many gonochoristic species can use **water**: permits the simple release of sperm and eggs, is an important way to the sperm transfer*
- planktonic gamete production often involves **simultaneous spawning**, both *male and female release in the same moment the gametes (eggs and sperms) in the water in order to allow them to the combination of the gametes: the organisms that release the garments directly into the water are called **SPAWNER INDIVIDUALS**.*

E.g. *coral spawning*: corals have separate sex, they are gonochoristic, but some species are hermaphrodite. Corals during the reproduction period release all the gametes (in the same night on the year), during this night, (is unknown why it is selected), the **water becomes red** (is full of gametes, to maximise the probability of fecundation). At the end the fecundation happens into the water column.

HERMAPHRODITE SPECIES →

- Species that produce gametes (sexual products) of both sexes during an individual's lifetime: the same individual could be in the same time both male and female
- 2 sub-categories of hermaphrodities:

SIMULTANEOUS HERMAPHRODITIES: the sex cells for both eggs and sperm are active within a single individual at the same time, but the **self-fertilization is rare**, even if is technically possible, e.g. *Acorn barnacles* possesses both the sexual organ, penis and ovary, even if the self fertilization never occur, they are sessile, so they use the long penis to copulate and at the same time it can receive and donate gametes → ADV: don't have to spent energy to find the partner because male and female is the same, it is always the complementary sex

E.g **Indigo Hamlet** is another simultaneous hermaphrodite: it lives in the Caribbean Sea, is a fish, to avoid the self-fertilization use a strange behaviour: egg trading → after meeting in the same spot of the reef, in the Caribbean Sea, the pair of hamlets rises in the water column and the fish acting as a male embraces the one acting as a female releasing sperm, so the male release sperm and the female eggs (lasts a few seconds), after the pair goes back to the reef and after few minutes they rise again, but now the roles are reversed (male-female), this strange spawning behaviour occurs just before sunset

E.g **Marine Flatworm** is another simultaneous hermaphrodite: they use a "Crude copulation act" trying to stab the partner with penis and stylets outward, after there is a hypodermic insemination → the individuals fight to be the male and try to stab the partner injecting the sperm on the skin, who win act the male, the other one the female

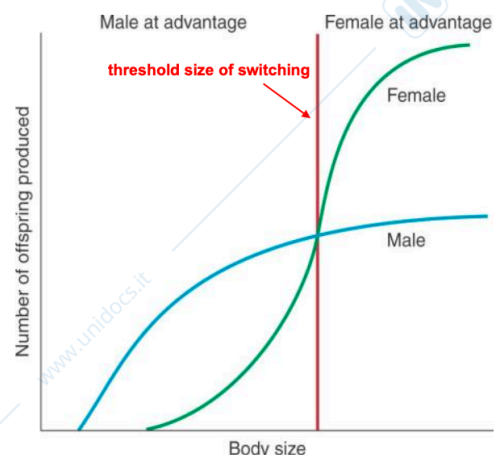
SEQUENTIAL HERMAPHRODITES: they start their mature sex life as one sex (male or female), and then they transform into the opposite sex (male or female), they don't have the possibility to produce at the same time both gametes, but they can produce them into 2 different live's phases
Within this category there are other 2 types of species:

- **PROTANDROUS SPECIES:** they start their life as male, after a specific period they became female (e.g. polychaetes, prawns and oyster), E.g *Crepidula fornicate* is a snail that occurs in stock, we have the larger (the older) that is the female and lives below, instead the younger (the male) stays on the top, in the middle there is the transitional form
- **PROTOGYNOUS SPECIES:** they start their life as female, after became male (e.g. coral reef fishes), in fact the older organisms in the female, in addition to change the sex, many coral reef fishes change also the colour

Which are the advantages to change sex during life? We condor here the case of:

Protandry → **SIZE ADVANTAGE MODEL**

- As a general rule → Producing eggs costs more energy than producing sperm, so larger and older animal has more energy at its disposal than a smaller and younger
- It would be best to be **male** while still *small* (then when is older), because a relatively small investment in sperm can produce many offsprings: BEGINNING
- When reach a specific body size, called **THRESHOLD SIZE OF SWITCHING** (is that size at which the number of offspring produced is the same regardless all the sexes, below



the animal produces more offspring if is a male, above it produces more offspring if is a female), the females are able to produce more eggs, so there is the change of sex: MIDDLE

- Above a certain threshold size (and age) **female** can produce more offspring because the available energy can be used to produce more eggs: AT THE END

Protogyny → ADVANTAGE

- As a general rule → the protogyny adaptation behaviour is used by these species that use to compete with other males for the female, in fact they usually that bright colours, rapid swimming, more energy, are bigger... these characteristics allow more success in the reproduction and to be chose by the female → this strategy is advantage when the species have to fight and compete for mating, as *coral reef fishes*
- Usually are rapid swimmer because this led to be more attractive to the female, many tropical fishes are protogyny also because are able to fight and win against other organisms
- Advantage to be male later considering the common role of males as competitors for mating
- Success as a male often entails agility at combat, bright colours, rapid swimming and these traits are enhanced with increased size and experience
- Important when aggression is important in mating success, e.g., some fishes where males fight to maintain group of female mates

HAREM: e.g. *Anthias* the largest fish is more coloured, bigger and male, it control the harem composed by other small females. When the male dies, the older female became male changing sex

Fertilisation success

is affected by:

- the mode of sperm transfer
- the volume/amount of gametes produced
- the distance between male and females
- behaviour
- timing

Focus on... **SPERM TRANSFER**

Different specialised means of sperm transfer, there are 3 different way to transfer the sperms to the eggs:

1. **direct contact** → apply sperm to the body surface or egg clutch (aggregation of eggs exposed to the external medium by the pompom crab: the male directly apply the sperms to the eggs). The fertilization success is not very high because same material can be lost in the environment
2. **copulation** → it increases the probability of fertilisation because there is no release of material in the environment, e.g many mollusks have copulatory organs: Cuttlefish use a **tentacle** to transfer
3. **Free spawning** → release of the sperm directly in the water, so many species take advantage to the presence of the water, in order to increase the % of fertilisation success, the sperms are more numerous then eggs, there are 2 types of spawning:
 - Species that use **epidemic spawning process:** e.g. mussels → when an organism starts to spawn, the other organism starts to spawn (the stimulus of one spawner causes other individuals to shed gametes)

- Species that use **mass spawning process**: e.g. coral species, sea stars → all the corals, sponges or sea stars of a specific area, in a single night decide to spawn without a signal, as the species before

FREE SPAWNING: Although free spawning has a very high fertilisation success (often exceeding the 90% because produce more sperm than eggs) there are also *significant costs and problems* relating to:

- **Population density and n° of individuals** → with a low population density and low number of individuals we have a low fertilisation success (high fertilization success is reached with high density and high number of individuals)
- **Water turbulence and current flow** → the currents are necessary for the gametes encounter, but they must be not so strong, otherwise the recognition between the 2 gametes is impossible
- **Polyspermy**: many sperms may simultaneously encounter a single egg, this can be a problem, even if usually or the animals have some mechanism to avoid and block the polyspermy and to prevent that a lot of sperms fertilise a single egg
- **Timing of egg and sperm release** → must be simultaneous with intraspecific signals (e.g lunar cycle for the corals) that induce the release of the gametes

Other organisms that spawn are also FISHES, groupers, indigo hamlet...

GROUPERS SPAWNING: Group of fish which have interesting reproductive habits, in particular, e.g *Epinephelus striatus* (*Nassau groupers*, *cernia striata*) live maybe in the Caribbean Sea, they aggregate in a specific part of the reef and thousands of organisms can meet, then for spawning release the gametes, unfortunately for some population is know the tie and the place where they spawn, so for the fisherman is a good opportunity to catch. They are protogynous species, so if the fisherman catch the bigger individuals, they release all the male causing a change in the structure of the community (only female, change in sex.)... moreover the groupers are files a lot because are very palatable, in fact a lot of species of groupers are into the red list the UCN. They can travel for 200km and meet a lot of organisms (when they can meet there could be more than 200.000 individuals)

Planktonic sperm and eggs

There are 2 main phases in gamete encounter:

- 1) Attraction of sperm to eggs by means of **sperm attractants** (es. aminoacidic compounds) which surround the eggs es. **acid L-tryptophan** (in red abalone), pheromone **Lamoxirene** in Laminariales (involved as sperm attractants is the kelp)
- 2) When the sperm reaches the egg, involving a complex set of chemical signals between the eggs and sperm to **avoid interspecies fertilisation using binding proteins** (sperm acrosome) receiving **proteins** (egg membrane) to allow to the sperm to fertilise the egg

Urchins: **bindin** protein in acrosome, binding receptors in egg cell membrane (ECM)

Abalone: **lysin** protein in acrosome creates hole in ECM

Parental care

Marine species which reproduce sexually, can also to parental care (females or males) take care for *eggs*, *embryos* and *young*s:

- *Gasterosteus aculeatus*: the male has red colour during courtship to lure females to lay eggs in its hidden nets

- *Trigger fish* produces benthic eggs release at the bottom, then the male control the water column and fight against who try to move within this area (is a matter of protection)
- *Gemma gemma*: nurtures its young within the mantle cavity and releases them as shelled juveniles
- *Apogon sp*: male incubates eggs in its mouth, when the eggs are ready to produce the offspring, they are release to the mouth of the male
- *Uca crab*: female incubates eggs for 2 weeks before release larvae
- *Seahorses*: after 3-4 days of courting, the male releases and produces the offsprings, the youngs, they are release directly from the main pouch (are viviparous species). The female injects the eggs into the male, when the babies are ready, from the hole of the male the organisms are released.

ASEXUAL REPRODUCTION

Many marine organisms are capable of reproducing without the formation of a zygote, or they can combine the two types of reproduction according to the environmental conditions and the life period.

ADV:

- There is lack energy spent compared to the sexual reproduction
- Is a rapid way to spread the genotype in the same habitat that has successfully colonised a habitat
- There are 2 common ways of asexual reproduction: **Fission** (or fragmentation) or **budding**

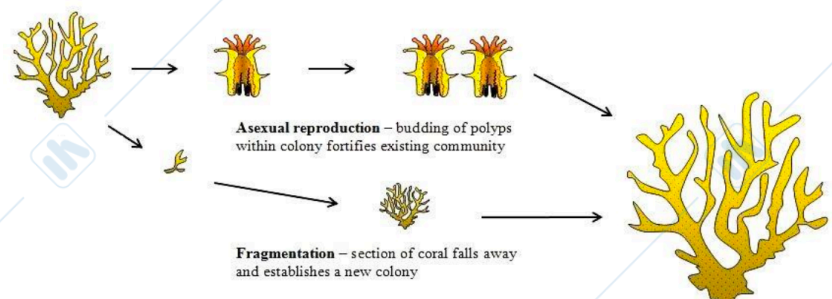
DIS: **There is no exchange of genes, there isn't a genetic mixture**

Descendants are genetically identical: **CLONE**

- **Colony**: it is group of organisms that live together and are genetically identical. A colony can also be defined as a **module**, each module (each organism of the colony) may be produced from a sexually formed zygote, e.g. corals are composed by many polyps that derive from an asexual reproduction, so the formation of a larvae that was created after a spawning event. The first polyp create the colony asexually. These organisms are called **MODULAR ORGANISMS**, e.g. coral, sponges, some ascidian, sponges (composed by singular organisms that are clones), seagrasses live in colony (in the seagrass bed, if I have one species, all the organisms of a single plant that create the seagrass bed have the same DNA)

Coral asexual reproduction – BUDDING

Starting from a single polyp which was generated by a sexual reproduction event (following the spawning during the night), by budding a little polyp starts to grow starting from the first polyp, so from 1 polyp, we obtain 2,3,4 polyps, increasing the size of the colony. The same can also occur by fragmentation, if there is a piece of broken coral, a branch, starting from this branch other polyps can grow increasing the size of the colony



→ the corals combine sexual (only 1 or 2 time per year) and asexual reproduction

Anemone asexual reproduction – BINARY FISSION

Anemone, as the bacteria can reproduce with a binary fission event, so the anemone grows, after it decides to divide itself in two different anemones that are genetical identical, are clones

2 – MIGRATION

A lot of organisms can migrate to different location showing a reproduction and migration cycle:

Juveniles drift from the spawning area (where they born) to the **nursery area** (when they spent time as juveniles), then they move to an adult **feeding ground**, also called adult stock where they became adult and then they move to the **spawning area** to reproduce. Between the adult stock and the spawning area there are 2 ways arrows, in fact the adult can migrate more than 1 time to the spawning area to spawn

Looking the migration type, we can divide organisms in different categories

1. **Diadromous species** → species that divide their live between freshwater parts of estuaries and in the open sea, (they live both in the freshwater estuary and open sea), they could have:
 - a. ANADROMOUS LIFE CYCLE: e.g. Salmon, Sea Lamprey → they spent most of the time in salt water, in the open sea, but they migrate reaching the freshwater of the estuaries to spawn during the reproductive phase of the live, the juveniles grow in freshwater and then when they became adult they move to the sea and the cycle restarts
 - b. CATADROMOUS LIFE CYCLE: e.g. Eels → they spent the adult life in freshwater, in the estuaries (intertidal zones), then they move to the open sea to spawn during the reproductive phase of the life, the juveniles grow up here and then when are ready return to the freshwater and the cycle can continue. There are 2 species of Eels, *Anguilla rostrata* – American, *Anguilla anguilla* – European: both migrate from the freshwater to the ocean sea, they move to spawn in a partially overlapping area in the Sargasso Sea. This trip to the spawning area is very unknown. Then the American eel move to the American rivers, instead the European eels continue to drift across the Atlantic Ocean, are carried by the currents into shallow water also reaching the Mediterranean Sea, when these larvae reach an estuary became juveniles, and metamorphozise into a GLASS EEL: juvenile of the eel. Since both the species breed in the same area (Sargasso Sea) sometimes is possible to find HYBRIDS of the 2 species, e.g. in Iceland
 - c. AMPHIDROMOUS LIFE CYCLE: e.g. Bigmouth sleeper, Mountain mullet → they born in freshwater, then they go to the open sea as larvae and return back to the freshwater to became adult and spawn there into the freshwater.
2. **Fully oceanic species** → many marine species stay always into the salty water, but they can migrate in different parts of the ocean. They feed and breed near the oceanic coast or in the open sea, although they migrate between different localities: e.g Cod, Herring, Green turtle, Plaice, Humpback whale
 - d. OCEANODROMOUS LIFE CYCLE: e.g. Mutton snapper, Black grouper, Herring → they are species which show a migration pattern between the home reef and the spawning grounds without having a nursery area. Herring, *Clupea harengus* borns near spawning grounds (coast of England), then when is grow it moves to the deeper water and feeds upon larger zooplankton reaching the coast of

Canada. They return to spawning ground after 1 year. The warring live in different stock, in different populations that follow different migratory routes.

The green turtle – *Chelonia mydas*

Is clear that they are fully oceanic species, that they migrate from the feeding area to the coast of the beach for a lot of km where they lay the eggs, but is not completely known these 2 points:

1. **How they are able to find the beach?** In a small scale it seems that sea turtles are able to respond to the light and wave actions in order to find the water. Right now the evidences suggest that there is an imprinting of the born and for this reason the females go to the same beach to lay the eggs
2. **What is the mechanism of migration routes?** In a larger scale, it seems that the perception of the earth magnetic field can be used by the turtles as a map, as a sensor.

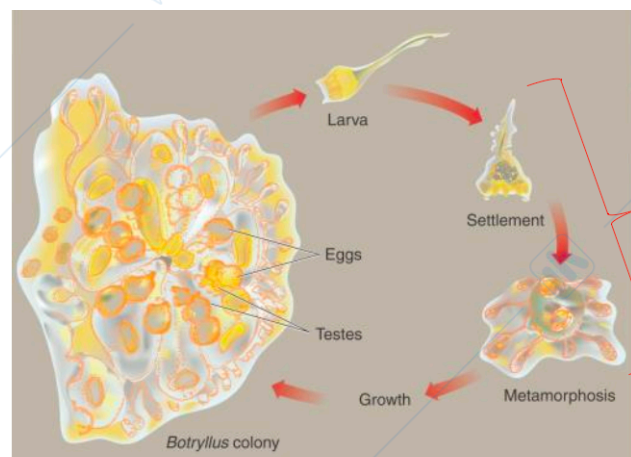
HOW CAN WE STUDY MIGRATION? We can use different instruments, tags

- ❖ **Implanted tag** → permanently or semi-permanently placed inside the organisms by a surgical implant. They are more invasive, but there is a continues transmission of information, of data, so they cannot be lost. But we can't use if for large fishes that swim vary fast or that swim in a great depth because we an lost the signal.
- ❖ Using **acoustic tags** → develop to be attached to the skin of large organisms, mammals, turtles, by means a connector that rust out and release the tags after several months, usually it provide also the T or other abiotic parameters of the water
- ❖ Using **pop-up satellite tags** → develop to be attached to the skin of large organisms , mammals, turtles, by means a connector that rust out and release the tags after several months, usually it provide also the T or other abiotic parameters of the water

Thanks to this tags we can also create MAPS of the different migratory routes of turtles, sharks, whales, tunas, seals, seabirds.

3 – LARVAL DISPERSAL

The characteristic of laurel production and dispersal is a **Complex life cycle**: there is an adult stage following by a sexual reproduction, larvae are produced, then there is the dispersal of larvae, they can move to new sites by the water currents and can settle there. The settlement is very important, it is the colonization of a new area when a larvae starts to metamorphose (acquires the morphological structure of the adult). When the metamorphosis is finished, it starts to grow until reaching the reproductivity maturity and produce new larvae...



The **settlement and the metamorphosis** to an adult is called **RECRUITMENT** → is the final arrives at a site (settlement) and metamorphose

Example of a complex life cycle of a marine invertebrate with a dispersing phase. The colonial sea squirt (sea ascidian) *Botryllus schlosseri* is a colonial hermaphroditic species. Sperm move through the water from

one colony and fertilise a nearby neighbour. Larvae emerge and move only a few meters to settle, metamorphose, and establish a new colony

3 different types of INVERTEBRATE LARVAE looking the different types of dispersal distance

1. Larva that are direct release next to the adult:

- Many species use this type of dispersion of the larvae
- This is the shortest type of dispersal
- viviparous species (they **release the youth directly** into the water, are large, but are already similar to the adults, they are mini adults)
- oviparous species (they produce **young hatch from eggs**) → release just next to the adults

e.g *Littorina saxatilis* (viviparus)

2. Lecithotrophic larvae:

- female produces not so many eggs (close to 10^2 to 10^3 eggs) but they have a large size
- These larvae depend for the nutrient from the egg yolk (red part of the egg), don't taking food from the environment, for this they don't have feeding or digestive structures
- Some of them have ciliary bands used for locomotion, they move not only thanks to the currents
- They are capable of limited swimming (can move only for 10-100 m) and short dispersal time (before the settlement they can move just for few hrs per days)

e.g of a lecithotrophic larva of the colonial ascidian *Botryllus schlosseri*. This larva lives for only a few hours, is a poor swimmer, and moves only a few meters from the parent colony

3. Planktotrophic larvae:

- The female produces many (10^3 to 10^6) small eggs (some species are able to produce million of eggs)
- they start feeding the egg yolk, but then they feed on the plankton because spent a lot of time in the ocean, so the yolk is not enough.
- Since they eat plankton they have specialized feeding structures and digestive systems
- Have long dispersal time (can spent one to several weeks before the settlement into the sea)
- some are very long distance (called **teleplanic larvae**) → they cover long distance and are able to cross the entire ocean
- They have different development proceeds, different stages of development (planktonic stages)
- They have ciliary bands used to move and feed upon the planktonic food

There are other species that have more than one larval development modes, they can produce both lecithotrophic and planktotrophic larvae → **poecilogonic species**

e.g Larva of the red sea urchin *Strongylocentrotus franciscanus*. Dark pigment spots are concentrated near the ciliary bands used for feeding and swimming.

Modes of dispersal of BONY FISHES LARVAE

- They are different from the three different categories of larvae that we have seen before because mostly all the larvae of fishes show the same behaviour, **they remain in the water column**, in particular in the surface (top part of the water column), from 2 weeks to several months, then they

start the **metamorphosis** reaching the coral reef (if they belong to tropical species) or the bottom or other bent ecosystem (if they live in other latitudes)

- Most marine fishes species spawn buoyant eggs (have a positive behaviour in the water) and sperm into the water
- The embryos first develop into larvae with a prominent yolk sac: is the nutrient of the organic, in a big transparent hole in the bottom of the fish used in the first stage of the larval development
- Once the sac is absorbed (completely used) the larvae feed on zooplankton: they have an primitive but effective digestive system to feed on zooplankton
- Larvae remain in the upper water column from 2 weeks to several months before metamorphosis

e.g Coral reef fish larvae are not able for their rapid swimming speeds related to a need for reaching more specific final habitats

reproductive timing and egg size

Larval production must often be timed precisely to allow settlement and promote dispersal, it is important:

- to avoid being swept to inappropriate habitats: is important to reach the habitats of the species
- to avoid counter predation: Ideally, larvae should be released during high tide and at night to be in the dark to avoid predators...E.g *Pomacentrus chrysurus*: is a small fish that lives in the coral reef, it lays the eggs during the sunset to avoid the predation

Variation in egg size and number may relate to different consequences in terms of mortality

Organisms that produce a high number of eggs, is because the eggs are highly subjected to predation

- **Size:** directly released juveniles > lecithotrophic > planktotrophic (they are smaller and are produced in higher number, but the mortality is higher)
- **Number:** planktotrophic > lecithotrophic > directly released juveniles (they produce less number of larvae because they are able to survive better since they have a big size)
- **Mortality:** planktotrophic > lecithotrophic > directly released juveniles → the mortality follow the same relationship and trend of the number of larvae → the planktotrophic larvae since they swim in the open ocean longer than the other, show much higher mortality rate

The micro-scale: settlement and metamorphosis

Larvae capable of settlement and metamorphosis are said to be **competent**: larvae reach the final habitat and then start the metamorphosis → when a larvae start the recruitment, it is called competent

Different settlement stages:

1. There are one or more stages of **Light** (photopositive or negative behaviour) and **pressure** to maintain depth for optimum feeding (in surface) and location off settling sites (on the bottom). Larvae usually have a swimming organ → larvae are able to sense the light and the different pressure in order to move, remain in the upper part of the water and reach the bottom during specific development stage
2. After touching the bottom, they must understand which type of bottom is optimal for the development, so larvae use **chemical and mechanical cues** to detect **suitable settling substrate**.

Usually a suitable settling substrate is a substrate with bacteria that can allow the live and with determinate physical and hydrodynamical characteristics of the substrata

e.g. Rock-dwelling barnacles larvae move to surfaces with pits and groove which provide secure attachment against wave action, predation and competition

3. In **gregarious settling**, larvae settle themselves on adults of their own species, they are able to localise them and settle on them, they are attracted by members of the same species: These larvae usually require direct contact of larvae with adults because the chemical cue is a soluble or insoluble peptide or other molecule (Arthropodin in barnacles) use as a way to attract other larvae

- ADVANTAGE: gregarious settling allows a larva to settle in a site where adults have already settled and survive, is a good environment because other species live there
- DISADVANTAGE: the larvae can be eaten by adults of the same species (adult attract the young in order to feed on them), predatory behaviour

4. **Settling on other species by chemical and mechanical attraction**

- In the opposite of the gregarious settling because there are larvae that settle themselves on adult of other species, they are attracted and this *is driven by chemical and mechanical attraction*
- *Mytilus edulis* larvae (cozza) are attracted to filamentous red algae, so they use these algae as substrate for the growth; in an experiment they try to replace the filamentous red algae with rope (have the same texture of the red larva) to see the differences and see that also mechanical attraction can be used, in fact the mytilus was attracted in the same way (are not only the chemical properties which attract)
- Some animals can release chemical to inhibit the settlement of other larvae → (*negative chemical interactions*)
- After settling, larvae may move a short distance, no more than a few cm, to a better site and to have space from others (this mainly for the spaces that create aggregation, e.g. mytilus)
- Larvae of the hydroids (*Proboscoidactylidae*) settle on the tentacle of the annelid worm (*Sabellidae*) and after settling they live as adult on the tube
- Some bryozoan larvae are attracted to seaweeds by chemical substances

5. **Larva metamorphoses into an adult stage** (is the last step of live)

- During the metamorphosis the larvae change completely the aspect becoming an adult
- The energetic cost of metamorphosis sometimes is very high, often is so severe that the animal must feed immediately afterward (not all the animals can reach the final stage, they can die before)

Settling and metamorphosis of *Pocillopora damicornis* larvae (larvae of coral)

Note the rows of zooxanthellae. This larva can live in the plankton and are competent to settle and metamorphose for periods greater than 100 days because they have symbiotic zooxanthellae which fuels the larva's journey over long distance across the open ocean. Planulae: starting from the gametes release into the water through the spawning, after the fertilization, this little larvae of the coral starts to swimming and reach the substrate, then fixed and the larvae starts the metamorphosis and becomes polyp. The larva already has the zooxanthella inside the body (fundamental for the photosynthesis, for the food acquisition). From a polyp we can create other polyps through the process of asexual reproduction, budding process and the colony can grow becoming after a lot of years, a big organism

The meso-scale: **transport by currents, loss of larvae**

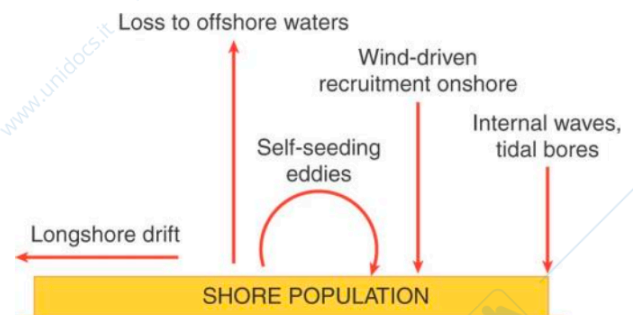
The vast majority of the planktonic larvae never reach the destination, they die before or are lost in not suitable environment.

Planktonic larvae suffer extensive mortality from:

1. Predation
2. transport to inappropriate habitats
3. starvation (lack of food)

Planktonic dispersal success of marine species is strongly controlled by **currents** that transport larvae and may have important ecological consequences. Es: species with planktonic larvae are relatively rare in Galapagos.

General possibility of larval transport: depending on the local currents the larvae might be swept of offshore waters (loss to offshore waters), they might be bring on shore by the waves that moves the shore, sometimes longshore drift can move the large in other directions... Depending of the tidal regime, the currents, the behaviour of the larvae can change a lot, they can be loss and never reach the final habitat. In fact species that use planktonic larvae are rare, e.g. in the Galapagos where there are a lot of currents, there are few species that produce planktonic larvae.



What happen to the species that live in estuarial habitats? 2 different behaviours

ESTUARINE LARVAL ADAPTATION

Many estuarine species live within an estuary, but **some larvae and juveniles may spend some period in coastal waters** in order to **avoid predation** (in the estuarine we can find large predator)

Estuarine circulation:

- **On the surface there is the freshwater (less dense) it flows seaward (far from the coast), whereas the more saline bottom layer moves landward (near the coast):** If the estuarine planktonic larvae held their position near the surface they would be carried out to the sea

1. Estuarine retention: larvae don't leave the estuary

1. if the larvae stay in the surface, they can be carry out the coast, to the sea, but sometimes the larvae can change the behaviours, they remain inside the estuary because are able to rise on the flooding tide (the water from the sea go inside the estuary, the larvae remain In the surface) and sink to the bottom on the ebbing tide remaining in the estuary. But they must face a very intensive predation pressure (is higher than in the open sea), so these larvae usually developed defensive mechanism: e.g. erectable spines → larvae of the mud crab *Rhithropanopeus harrisi* have erectable spines, which make it very difficult for fishes to attack: this is a necessary defence for larvae that are retained within estuaries, where predation by fishes is intense.

2. Coastal migration and return

- Larvae will spend the larval time far from the estuary in order to avoid the predation, so they may rise on the ebb to move offshore to coastal waters and then depend upon wind-driven currents to go back to the estuary.
- They are subject to a low predation (ADV) but there is a high probability that larvae will never return to estuary depending on the currents and the physical characteristic of the basin (DIS) → E.g Blue crab, *Callinectes sapidus*: the larvae rise during the flooding tide, then they sink and return back thanks to the currents

CORAL REEF FISH LARVAE

- Planktonic larvae of several weeks' duration: they spent several weeks far from the reef in the planktonic stage, in the middle of the ocean, many species are able to return back to the same reef of the parents, is a similar behaviour show by the turtles and the beach.
- Many species show strong evidence of adaptations to take advantage of currents to return to localised reef areas of their parents
- An experiment in Papua New Guinea analysed 2 different species of tropical fish:

E.g *Amphiprion percula* (is the clown fish, it spent only 11 days in pelagic habitat), *Chaetodon vagabundus* (is the butterfly fish, it spent 38 days in pelagic habitat). The first one is a short dispersive larvae fish, the second is a large dispersive larvae fish. How they are able to go back to the parents reef? They study this behaviour labelling females by injecting them with isotope of barium that was translocated to eggs and larvae, they can monitor the moving of the larvae; moreover they study this considering a the small island reserve (0.3 km²: small study area) we expected (though) that most larvae would be lost, INSTEAD **About 60% of both the species larvae returned to their native reef** → how are they able to do it? There isn't a common hypothesis, someone thinks that is due to the use of sound to locate habitats or the sun compass orientation or they are able to smell some characteristic of the reef, e.g. leaves. In another article they analyzed that when the eggs are released, they immediately start to go to the same direction staying in group, as turtle.

4 – PLANKTONIC LARVAE: Obstacles to the final destination

There are main **pre-settling problems** that the planktonic larvae must face:

- Food shortage (starvation)
- High concentration of toxic algae during a precise time of the year (phytoplankton bloom)
- Loss of larvae by currents
- Predation of the larva

A strategy adopted to reduce and avoid predation of the number of larvae:

CLONING (by asexual reproduction): *some larvae are already ready to reproduce themselves asexually (when they are in an environment with good condition, they are able to create clone in order to increase the size of the population, e.g. lot of food). E.g. Pisaster ochraceus, Seastar creates a bud (asexual reproduction), it starts to grow and another larvae will born* → this occur not for the adult, but for the larvae). In response to chemical cue from fish predators (e.g. sand dollar produce smaller clones to be less visible)

There are main **post-settling problems** of planktonic larvae (when they are in the final environment):

- Energetic cost of metamorphosis: is a very expensive process
- Predation
- Crowding: especially for species which create aggregation, they have the ability to move a little bit once settle, but sometimes this is not enough to avoid to be overgrown by other large of the same species and they can die

5 – THE MACRO-SCALE: the BIOGEOGRAPHY STRUCTURE

The macro scale is also known as the biogeographic scale:

- The geographic range of a species with planktonic dispersal is greater than the range for species without planktonic larvae and thus with direct release the juveniles close to them
- We can define **different geographic regions, zones**: where the animals or the plants distribution have similar or shared characteristics. They exist because there are physical or not physical barriers that affect the distribution of the larvae. e.g. for a specific species we can define 8 different geographic regions

Biogeographic barriers:

1. **Physical barriers** (any physical features)

- Broad ocean (Atlantic and Pacific)
- Separate current circulation coastlines
- Different density of the water
- Different T

2. **Strong natural selection** (is a natural barrier, it is strongly related to the physical barrier because it is a consequence of the physical barrier)

- if a larvae disperses to a location where it cannot survive normally or where its adult phase cannot survive (es: different temperature), then the individuals are liable to be isolated from the source of those dispersing larvae: in this case an intraspecific genetic difference occur that create this isolation between the population, creating 2 sub population, with the time, the isolation creates the speciation

NATURAL SELECTION → intra-specific genetic difference, this led to isolation between populations (sub-populations), so at the end there is the speciation